A Palaeozoic open shelf benthic assemblage in a protected marine environment

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ABSTRACT

A Late Ordovician benthic assemblage containing trilobites (*Colpocoryphe*, *Onnia)* and diploporid echinoderms (*Aristocystites*) taxa that are usually typical of open shelf environments is preserved in protected marine settings in the lower part of the Kermeur Formation (Armorican Massif, NW France). A facies analysis carried out on the Veryac'h section (Crozon Peninsula) allows identification of four sedimentary facies (SF), ranging from

the bay/lagoon domain (SF1 and SF2) to the back-barrier (SF3) and barrier (SF4) domains. A benthic fauna comprising trilobites, brachiopods and diploporids is found in the SF1 and SF2. In SF1, fossils are randomly scattered in sediments (taphofacies 1, TF1) showing two different preservation stages: TF1a with complete articulated skeletons and TF1b with disarticulated shells. These two preservation stages can be related either to the different modes of life of the taxa (i.e., recumbent, burrowing or nektobenthic) or to a composite assemblage with both autochthonous and allochthonous taxa. In this benthic assemblage, some trilobites and echinoderms taxa are mostly preserved either as complete exoskeletons and exuviae (*Colpocoryphe grandis*) or complete thecae (*Aristocystites* sp.), indicating an autochthonous origin. These taxa are usually found in low-energy open shelf settings. Their occurrence in a protected environment results from the combination of both allocyclic factors (i.e., change in sea level) and local conditions (i.e., shelf morphology, environmental conditions). Indeed, the lower part of the Kermeur Formation was deposited during a transgressive phase following a significant sea-level fall (Sandbian–Katian boundary). During the transgressive phase, barrier-lagoon systems were formed on the flat surface inherited from the sandbian shelf. Under non-restricted ecological conditions (i.e., normal oxygenation and salinity) in the protected settings, the new ecological niches were suitable for benthic organisms accustomed to open shelf environments. The settlement of these open shelf benthic species in coastal and protected environments may represent an offshore–onshore expansion, contrary to that described in the onshore–offshore diversification model of Phanerozoic shelf communities (Jablonski et al., 1983 ; Sepkovski, 1991).

Keywords: Barrier-lagoon environments; taphonomy; facies analysis; Katian (Ordovician); Armorican Massif.

1. Introduction

Numerous studies have been carried out on Ordovician shelf successions belonging to the northern Gondwana margin in order to explain the relationships between benthic fauna distributions and related depositional environments. Results from these studies have led to the recognition of "biofacies" or benthic associations along an open shelf profile, especially for trilobites (Fortey and Owens, 1978, 1987; Henry and Destombes, 1991; Vidal, 1998; Zhou Zhiyi et al. 2001, 2003; Turvey, 2005) and brachiopods (Villas, 1985, 1992, 1995; Havlíček, 1989; Havlíček et al., 1987). These biofacies are valuable tools for palaeogeographic reconstructions (Fortey and Owens, 1987; Henry, 1989; Henry et al. 1997; Fortey and Cocks, 2003).

The present work shows that, in some particular contexts, benthic taxa that are generally associated with open shelf environments can also be associated with marine protected depositional settings. The Upper Ordovician succession studied here is located on the Crozon Peninsula (Armorican Massif, western France). Sediments were laid down during the sea-level rise following the major sea-level fall recorded in the *foliaceus* graptolite zone (Sandbian–Katian boundary; Webby et al., 2004). This regressive event is recognized in several areas of the northern Gondwana Domain, from the Armorican Massif (Robardet, 1981) to the Iberian Domain (Portugal: Henry et al., 1974; Paris, 1979, 1981; Spain: Villas, 1992), as well as the Algerian Sahara and central Morocco (Videt et al., 2010) and other palaeogeographic domains such as Baltoscandia (Nielsen, 2004) and Laurentia (Turinian–Chatfieldian boundary: Ross and Ross, 1992). In the northern Gondwana Domain, the fall and successive rise of the sea-level coincided with a decline in the endemicity of benthic fauna and the arrival of taxa from Avalonia, Laurentia and Baltica (Havlíčcek, 1989; Cocks and Fortey, 1990; Young, 1990). In the Armorican Massif, the transgressive phase led to the deposition of nearshore successions yielding a poorly diversified benthic fauna (Robardet et

al., 1994).

The aims of the present study are to (1) identify the depositional environments of these successions, (2) investigate the origin, either autochthonous or allochthonous, of the benthic taxa, and (3) understand the mode of settlement of organisms during the transgressive phase. The analysed successions comprise the upper part of the Postolonnec Formation (Sandbian) and the lower part of the Kermeur Formation (Katian). An integrated approach involving facies analyses combined with palaeontological and taphonomic observations (e.g., faunal content and preservation mode) is carried out.

2. Geological context

In the Armorican Massif (Fig. 1), the lower Palaeozoic terrains are subdivided into two palaeobiogeographic units: the Medio-North Armorican Domain (MNAD) and the South Armorican Domain (SAD). In the MNAD, several transgressive-regressive cycles occurred in the Ordovician (Paris et al., 1999; Paris et al., 2007; Dabard et al., 2009). The first transgressive phase began in the Floian (Early Ordovician) with the deposition of continental and/or coastal plain facies, and then several cycles succeeded each other in the overlying silty clayey formations until the late Sandbian regressive phase. In the Crozon Peninsula (Fig. 2), the Floian is characterized by thick sandstones of the Grès Armoricain Formation that were deposited in nearshore settings (Durand, 1985). These sandstones are overlain by silty-clayey shelf facies of the Postolonnec Formation, which is Dapingian to Sandbian in age (Paris, 1990). Then, the clastic sedimentation continued into the Katian with micaceous sandstones, quartz-arenites and mudstones of the Kermeur Formation (90 to 450 m thick; Plusquellec et al., 1999). In the studied area, this formation is overlain by the Cosquer Formation, dated as Hirnantian (Bourahrouh, 2002), and interpreted as glacio-marine deposits (Hamoumi et al.,

1981). The Postolonnec, Kermeur and Cosquer formations were deposited under stable platform conditions and were affected by weak deformation (Rolet et al., 1986; Darboux, 1991) and low-grade metamorphism (Paradis, 1981) during the Late Devonian–Early Carboniferous.

The diversity of the benthic fauna is variable in these Ordovician sediments. The Postolonnec Formation yields numerous and well-known macrofossil assemblages (Mélou and Plusquellec, 1975a) comprising trilobites (Henry, 1980), brachiopods (Botquelen and Mélou, 2007), bivalves (Babin, 1966), ostracods (Vannier, 1986a, 1986b), graptolites (Philippot, 1950; Henry et al., 1976), echinoderms (Chauvel, 1941; Chauvel and Nion, 1969) and gastropods. This diversity is reduced to only a few species in the overlying Kermeur Formation, including brachiopods and trilobites (trinucleids and dalmanitids; Henry, 1980) that are reported only from the upper part of the formation. The lower part is characterized by abundant bioturbation with few brachiopods and echinoderm plates (Mélou and Plusquellec, 1975a, 1975b, 1980). New material sampled by the authors reveals a higher benthic diversity than previously known.

3. Stratigraphic context

The upper part of the Postolonnec Formation (Fig. 3) consists of clayey silty facies containing sandy beds with hummocky cross-stratifications or siliceous and/or phosphatic concretion-bearing beds and shellbeds. It was deposited in a shelf environment dominated by storm wave action, between the median part of the inner shelf and the outer shelf (Loi et al., 1999; Loi and Dabard, 2002; Dabard et al., 2007). The bioturbation structures are small and primarily represented by *Planolites.* Macrofaunas are either randomly dispersed in the clayey siltstones or concentrated in shellbeds. Two types of shellbeds *sensu* Botquelen et al. (2004)

can be distinguished: (1) type A, 1 to 5 mm thick, lenticular and made up of a single coquina level; and (2) type B, up to 20 cm thick, continuous and composed of several superposed and amalgamated coquina levels. Trilobites (*Marrolithus bureaui*) and chitinozoans (*Lagenochitina ponceti, L. deunffi and L. dalbyensis* biozones; Paris, 1990; Paris et al., 1999) yield a Sandbian age for the upper part of the Postolonnec Formation.

The Kermeur Formation overlies the Postolonnec Formation without apparent angular discordance at the outcrop scale. The lower bounding surface is sharp and erosional. It is overlain by a conglomeratic unit, 40 to 70 cm thick, containing numerous ferruginous (Fe) oolites and phosphatic (P) pebbles (Deunff, 1958; Henry et al., 1974; Paris, 1981). The chitinozoans present in the conglomerate matrix belong to the *Euconochitina tanvillensis* biozone (Paris, 1981; Bourahrouh, 2002) from the lower Katian (Webby et al., 2004). Different chitinozoan assemblages of Sandbian age have been observed in the P-pebbles (Henry et al., 1974; Paris, 1981); some belong to the *L. deunffi* biozone and others to the *L. dalbyensis* biozone. These microfauna data indicate a partial reworking of the upper part of the Postolonnec Formation linked to the late Sandbian–early Katian sea-level fall (Paris and Le Hérissé, 1992).

4. Material and Methods

The Postolonnec and Kermeur formations crop out in the Crozon Peninsula along the Mort-Anglaise, Veryac'h and Poul sections (Fig. 1). This study was carried out at the Veryac'h beach, where these formations are both continuous and exposed in the sea-cliff. The high quality of exposure allows a facies analysis to be performed, including logging at the 1/40 scale. At the same time, palaeontological material was collected in the Kermeur Formation by excavation favoured by recent cliff-slides. Although macrofossils are rare and

scattered in these facies, about 90 specimens were collected. The diversity of the collected samples is similar to that obtained by amateurs over a period of a several years (M. Le Duff, personal communication, 2005). All specimens are housed in collections at the Geology Department at Brest University (prefix LPB), France. As most of the collected taxa have been previously described by Henry (1980) and Botquelen and Mélou (2007), only a few species are briefly discussed here at the end of this paper.

5. Facies analysis

Five sedimentary facies, SF0 to SF4, occur in the lower part of the Kermeur Formation.

5.1. Description

SF0: the basal conglomeratic facies contains Fe-oolites (mainly chamosite) and phosphatic pebbles (P-pebbles) in a bioturbated clay-sandy matrix made up of detrital quartz grains (150 to 250 µm in size) and phyllosilicates. The size of the Fe-oolites varies between 250 and 700 µm. They are deformed with a maximum elongation direction parallel to the bedding and some of them are broken. The P-pebbles, 0.1 to 2 cm in size, show an ovoid shape and display various compositions; some consist of microcrystalline apatite with detrital silt-sized grains of quartz and phyllosilicates and others contain coquinas with P-cement.

SF1: this bioturbated facies overlies SF0. It consists of beds with a constant thickness of approximately 1 m, made up of fine- to medium-grained clayey sandstones of a dark-grey colour ("dirty" sandstone); the argillaceous matrix makes up about 50% of the rock (Hamoumi, 1981). These sandstones are rich in quartz and contain micas and organic matter.

They are intensely bioturbated and the primary sedimentary structures have been destroyed. The bioturbation is less abundant in places, which leads to the preservation of some sandy layers (Fig. 4 A), 1 to 3 cm thick with flaser bedding, and some thin layers of black mudstone (approximately 1 cm thick). The well-diversified trace fossils are large (up to 3 cm in diameter). Most of them belong to the ethological categories of domichnia and equilibrichnia, (e.g., *Bifungites* and *Arenicolites*; Mélou and Plusquellec, 1975b), as well as some spiral systems (Fig. 4 B). In this facies, the fauna is scattered and scarce with the occurrence of some trilobites, diploporid echinoderms and very rarely, brachiopods. Some trilobite exoskeletons and diploporid thecae that are still articulated are preserved (see part 6.1).

SF2: this facies forms beds, 0.5 to 1 m thick, made up of intensively bioturbated sandy mudstones. The matrix (about 60% of the total rock) and organic matter are more abundant here than in SF1. Locally, the bioturbation is less abundant and primary structures can be observed. They are represented by thin (a few centimetres thick) black mudstones layers (Fig. 4 D) that can extend laterally over several decimetres and also by roughly laminated clayey-sandy beds with diffuse basal and top surfaces. Flaser bedding also occurs. The bioturbation, which is less diversified than in SF1, is dominated by numerous equilibrichnia structures (*Teichichnus*, 0.1 to 1 cm in width) that are distributed along the stratification (Fig. 4 C). This facies yields brachiopods, diploporids and only a few trilobite sclerites. Although the fauna is generally disarticulated and scattered, some rare lenticular shellbeds, made up of a single coquina layer, are present.

SF3: the bioturbated heterolithic facies is made up of well-sorted fine- to medium-grained sandy beds, several centimetres to 1 dm thick, that alternate with lenticular to flaser bedding (Figs. 5 A, C, D, E, F, G). The sandy beds show planar to subhorizontal laminations with very flattened hummocky cross-stratification (HCS) locally. The basal surface of the sandy beds is slightly erosive (Figs. 5 B, C) and preserves the crawling structures produced in

the underlying clay. Locally, weakly incised gutters and furrows are observed (Fig. 5 B). 2D current ripples (with a wavelength of several centimetres to 1 dm) and wave ripples (sometimes at the top of the sandy beds with HCS) are present in the lenticular to flaser bedding (Figs. 5 A, D, E). Current ripples showing opposite palaeocurrent directions (e.g., Fig. 5 E) and clay drapes within ripples (Figs. 5 A, D, E, G) are visible. Some wave ripples have flattened crests. Bioturbation is abundant but the stratification is preserved. It mainly consists of crawling structures (repichnia) that are preserved as hyporeliefs at the bases of the sandstone beds as well as numerous burrows (*Skolithos*) filled with clayey material (Figs. 5 F). This facies is devoid of body fossils.

SF4: this sandstone facies consists of medium- to coarse-grained and well-sorted quartz-arenite beds (1 dm to 1 m thick) with planar and low-angle laminations (Figs. 6 A, B). The beds contain numerous concave scours, draped by thin silty to fine-grained sandy beds, with a lateral extension from 1 to several metres (Figs. 6 B, C). Swaley cross-stratification (SCS) is observed locally (Fig. 6 D). The top surfaces of the sandy beds are flat and smooth, but wave ripples (wavelength of about 1 dm) occur within some sub-circular depressions (about 1 to 3 m in diameter; Fig. 5 H). At the outcrop scale, some beds pass laterally into layers with a flattened HCS belonging to SF3 (Fig. 6 C). Bioturbation (mainly *Skolithos*) is very sparsely developed. This facies is devoid of body fossils.

5.2. Interpretation

The P-pebbles of SF0 were provided from the underlying deposits. The late Sandbian sea-level fall led to a partial emergence of the shelf as well as the erosion of the nodule-bearing clayey siltstones occurring in the upper part of the Postolonnec Formation. During this regressive phase, the P-nodules were concentrated by winnowing and made up of pebbles

of lag deposits. Then, during the transgressive phase, these pebbles were integrated into the first Katian sediments.

In SF1 and SF2, the sandy fraction is relatively abundant (the mean values range from 40 to 50%), however no storm-related structures (e.g., HCS, silty laminae, coquina storm bed; Aigner, 1985; Botquelen et al., 2004) have been observed in the rare non-bioturbated intervals. Rather, the mudstone layers and flaser bedding in these intervals reflect alternating periods of quiescence and low-energy currents. Furthermore, some skeletons (carapaces or thecae) preserved in SF1 are still articulated or slightly dislocated (see part 6.1). These characteristics, together with the intense bioturbation affecting the deposits as a whole, are incompatible with sudden supply of sediments, yet imply low depositional rates with regular inputs. All these features argue against storm-dominated sedimentation in an open shelf setting, as can be observed in the underlying Postolonnec Formation (Dabard et al., 2007). Instead, they suggest a restricted environment, protected from storm influences, where sandy inputs are related to unidirectional currents or fair-weather waves.

HCS and SCS occurring in SF3 and SF4 are structures related to storm wave action (Leckie and Walker, 1982; Aigner, 1985; Brenchley et al., 1986). SCS (SF4) have only been described from shoreface environments (Leckie and Walker, 1982), whereas HCS (SF3) occur in spillover lobes in coastal lagoons (Shirai and Tada, 2000), open-coast tidal flats (Yang et al., 2005, 2006) and on open storm-wave-dominated shelves from the shoreface to the median part of the inner shelf (Dott and Bourgeois, 1982; Aigner, 1985; Guillocheau and Hoffert, 1988). In SF3, the wave ripples at the top of the sandy beds with HCS rule out inner shelf settings and are in agreement with nearshore settings. On the other hand, the occurrence of 2D ripples in lenticular to flaser beddings (SF3) and the preservation of clay drapes within current ripples imply alternations of periods of current activity and periods of quiescence. Such features are generally associated with environments submitted to tidal and/or fair-

252 weather wave processes (Reineck and Wunderlich, 1968; Sultan and Plink-Björklund, 2006;
253 Billeaud et al., 2007). A tidal influence is consistent with the opposite current directions (Figs.
254 5 E) observed in SF3. Moreover, it explains the preservation of wave ripples in sub-circular
255 depressions (SF4), which can be interpreted as puddles linked to a tidally-driven emergence in
256 a shoreface barrier. In these two facies, the association of storm-related structures with tidal-
257 related structures suggests a barrier context (e.g., Boyd et al., 1992; Dalrymple et al., 1992;
258 Cattaneo and Steel, 2003), where SF4 is interpreted as a barrier facies and SF3 as a back-
259 barrier facies (see the model in Fig. 7). The sandy beds, with planar and subhorizontal
260 laminations and very flattened HCS associated with small wave ripples (SF3), represent
261 deposits laid down when storm waves cut through and spilled over the barrier. These last
262 processes are emphasized in SF4 by concave scours draped by silt and fine-grained sand (Fig.
263 6 B). SF1 and SF2, deposited in an environment protected from storm influences, thus
264 correspond to bay/lagoon deposits (e.g., MacCarthy, 1987; Plint, 1988). In these facies, sandy
265 particles were supplied by continental areas (fluviatile system) and barriers (spillover lobes)
266 and were secondarily reworked by low-energy currents in the lagoon. The central location of
267 SF2 in the protected setting is supported by (1) the higher clay/sand ratio, which is consistent
268 with an environment far from a direct continental influence and (2) the occurrence of
269 disarticulated shells and rare lenticular shellbeds, which provide evidence of winnowings on
270 the bottom. The lack of evidence for restrictive conditions (e.g., hypersaline or anoxic
271 conditions) suggests extensive connections with an open marine environment, probably linked
272 to the discontinuity of the barrier and/or to submerged barrier portions. No indication of depth
273 (e.g., desiccation marks, wave ripples) has been found in SF1 and SF2. Bioturbation occurring
274 in the successive facies (SF1: *Bifungites*, *Arenicolites*; SF2: *Teichichnus*; SF3 and SF4:
275 *Skolithos*) is consistent with such depositional settings (e.g., marine lagoons and open bays;
276 Ekdale et al., 1984; Frey et al., 1990; Mangano and Buatois, 2004; MacEachern et al., 2007).

5.3. Stratigraphic evolution

The sharp-based contact and reworking of the underlying deposits characterize the transition between the Postolonnec and Kermeur formations. The lack of regressive facies is in agreement with a rapid and/or forced regression that led to the emersion and erosion of a segment of the shelf. Then, the first transgressive deposits were laid down during the Katian (*E. tanvillensis* biozone) on a flat surface inherited from the Sandbian shelf (the transgressive surface, TS in Fig. 8). This type of gently sloping shoreface-shelf profile allows the formation of coastal barriers (e.g., Beets et al., 2003; Dillenburg et al., 2004; Loi et al., 2010), which are built up from wave transport and sand accumulation along the coastline. In the Kermeur Formation, the basal transgressive deposits are represented by the bioturbated SF0, SF1 and SF2 laid down on a bay/lagoon setting. The superposition of back-barrier (SF3) and barrier sediments (SF4) indicates a landward barrier migration. This vertical facies evolution, from protected marine to open marine environments, is integrated into a transgressive evolution associated with a long-term sea-level rise (e.g., Heward, 1981; MacCarthy, 1987; Plint, 1988; Swift et al., 1991; Cattaneo and Steel, 2003; Yang et al., 2006). Higher up in the formation, several oscillations between protected marine and shoreface barrier environments can be identified (Fig. 3), gradually leading to an open marine environment later in the Katian (*Belonechitina robusta* biozone; Gorini et al., 2008).

6. Faunal assemblages and taphofacies

6.1. Description

In the lower part of the Kermeur Formation, fossils are only present in SF1 and SF2. Two different taphofacies are recognized, TF1 and TF2.

TF1: preserved in SF1, the fossil assemblage of this taphofacies (Fig. 9 A) includes trilobites, diploporids (echinoderms) and very rarely, brachiopods. The trilobites are assigned to *Colpocoryphe grandis*, *Onnia seunesi* ?, *Zeliskella* (*Zeliskella*) sp., *Phacopidina* sp. and *Eccoptochile* sp. The diploporids are assigned to *Aristocystites* sp., and the brachiopods to *Drabovia pentagonomya* (see below for systematic assignments; Botquelen and Mélou, 2007, for the brachiopods). The bioclasts are isolated and randomly dispersed throughout the thickness interval of SF1, without any ordered arrangement in the bedding plane and unrelated to sedimentary events. In this taphofacies, two different preservation stages (or taphonomic grades) for the fossils are distinguished, denoted as TF1a and TF1b, accounting for 60% and 40% of the material, respectively (out of a total of 46 specimens).

In the first grade (Fig. 9 A, TF1a), skeletons belonging to three taxonomic groups are preserved with different skeletal parts that are still articulated, each of them occurring as a single species. The trilobites include numerous complete exoskeletons and *in situ* exuviae (most of the specimens identified as moults correspond to a joined thorax and pygidium with overturned librigenae in the immediate vicinity; Figs. 10 A, B); this material is all assigned to *Colpocoryphe grandis*. The diploporids (Fig. 11), identified as *Aristocystites* sp., are preserved as scattered but complete thecae and a few isolated thecal plates. The brachiopods are represented by very scarce articulated *Drabovia pentagonomya* valves. These fossils are all preserved as internal and external moulds, without abrasion or bioerosion marks.

The second grade of this taphofacies (Fig. 9 A, TF1b) is characterized by a high degree of shell disarticulation, which are nevertheless always randomly dispersed; most of the material is composed of trilobite exoskeleton fragments, including trinucleids (*Onnia seunesi* ?, Figs. 10 E–H) and dalmanitids (*Zeliskella* (*Zeliskella*) sp., Fig. 10 G; *Phacopidina* sp., Fig.

10 F), along with less abundant taxa such as *Eccoptochile* sp. (Fig. 10 I), as well as scarce brachiopod valves (*Drabovia pentagonomya*, Figs. 10 L–M). These taxa are preserved only as isolated exoskeletal parts, and some specimens were broken before burial.

In summary, *Drabovia* occurs in both grades of this taphofacies, and *Aristocystites* and *Colpocoryphe* are mostly preserved as complete remains with different parts of their skeletons in articulated or slightly dislocated arrangements (Fig. 9 A; TF1a). *Onnia*, *Phacopidina*, *Zeliskella* and *Eccoptochile* are always disarticulated and/or fragmented (Fig. 9 A; TF1b).

TF2: preserved in SF2, the faunal assemblage of this taphofacies (Fig. 9 B) consists mainly of brachiopod valves, diploporid thecal plates (*Aristocystites* sp.) and very rarely, trilobite sclerites (Calymenidae, consistent with *Colpocoryphe grandis*). The brachiopods include three species: *Drabovia pentagonomya*, which is clearly predominant, *Tafilaltia destombesi* and *Triplesia* cf. *T. simplex*. This taphofacies is characterized by the preservation of fossils as lenticular shell concentrations on a single bedding plane. The lateral extent of these lenses varies from 1 dm to 1 m and their thickness can reach 3 to 5 cm. These lenses have a slightly erosive basal surface and consist of either a single thin coquina layer or scattered shells in a silty-sandy matrix. Bioclasts are preserved as internal and external moulds. All the specimens are disarticulated with a fragmentation rate of about 40% (based on 44 specimens), showing slight differences from one species to another (only the valves for which more than one half of the specimen is preserved were taken into account). No erosion, bioerosion or abrasion mark was observed on these fossils; however, their preservation as internal and external moulds in medium-grained sandstones makes it difficult to observe these features.

6.2. Interpretation

In the first bioturbated facies (SF1), the two taphonomic grades are associated but show two different preservation stages: TF1a with complete skeletons in an articulated position and TF1b with disarticulated shells. Grade TF1a contains trilobite exuviae preserved *in situ* and shows a very low degree of disarticulation, even when the skeletons are composed of numerous easily disconnected skeletal parts or plates. The physical integrity of arthropod carapaces belonging to grade TF1a indicates that the sediments were not disturbed (Plotnick, 1986; Speyer, 1991). These features, along with the scattering of fossils in the sediments, provide strong evidence that these fossils are preserved in their life environment. The assemblage of this grade is made up of *Colpocoryphe*, a trilobite burrower with predator/scavenger feeding habits (Hammann, 1983; Fortey and Owens, 1999a), and *Aristocystites*, a recumbent suspension feeder (Parsley, 1990). After death, the pre-burial position of *Colpocoryphe* provided protection from disturbance and disarticulation. A similar taphonomic result is observed for *Aristocystites*, whose complete thecae occur in the same habitat. This diploporid displayed a reclining mode of life on the sea-floor and its preservation was probably favoured by regular sediment inputs.

Conversely, grade TF1b is characterized by shell disarticulation. This cannot be linked to storm reworking because the shells are scattered in the sediments and coquina storm beds have not been observed. Two hypotheses can be proposed to explain this grade. The first one considers the modes of life. The disarticulated exoskeletons belong to epibenthic trilobites, (Fortey and Owens, 1999a, 1999b) including *Onnia*, *Phacopidina* and *Z.* (*Zeliskella*), and very rarely, epifaunal brachiopod (*Drabovia)*. The mode of life of these taxa exposes them to post-mortem disarticulation by scavengers, bioturbation and bacterial decomposition before burial. In some cases, the high proportion of disarticulation may be related to the morphology of the exoskeletons. For example, the distal tips of the trinucleid thoracic segments (such as in the genus *Onnia*) do not exhibit imbricated structures (Fortey and Owens, 1999b). These

trinucleid morphological characteristics favour rapid disarticulation compared to other trilobite families. Thus, the two taphonomic grades (TF1a and TF1b) of the benthic assemblage in SF1 can be interpreted as being related to the different modes of life of the taxa. A second hypothesis can be proposed to explain the occurrence of these disarticulated and partially fragmented shells. They could be allochtonous and transported by currents from open marine settings. In that case, these shells would be distributed in both fossiliferous facies, yet they were not observed in SF2; their relative scarcity can explain the lack of data in this facies. In this second hypothesis, the benthic assemblage of TF1 corresponds to a composite assemblage with allochthonous and autochthonous species.

In TF2, the coquinas are disarticulated and accumulated in lenticular bodies with a slightly erosive basal surface. This arrangement can be related to type A-shellbeds, as described by Botquelen et al. (2004), produced by the winnowing of the water-sediment interface that reworks the finer particles and leads to a concentration of shell debris. Two hypotheses can be proposed for TF2: 1) it corresponds to either a within-habitat time-averaged assemblage (*sensu* Walker and Bambach, 1971; Kidwell, 1998), considering the evidence for a low energy setting in this facies, or 2) to a para-autochthonous to allochthonous assemblage, considering the high degree of disarticulated shells and their accumulation in lenticular bodies. It is difficult to assess the degree of transport, but the interpretation of SF2 is compatible with limited reworking. In this case, the fauna could have drifted from more open environments such as inlets.

There are other differences between the faunal assemblages of the two taphofacies. Some taxa, although occurring in TF2, are either absent from TF1 (*Triplesia* and *Tafilaltia*) or significantly less abundant (*Drabovia*). These differences argue for a different origin for these assemblages, such as two different biotopes. This is especially relevant for the brachiopods, the abundance of which in SF2 could be linked to the substrate composition. Indeed, the

bioturbated sandy mudstones facies (SF2) could represent loose ground substrate, which is more favourable for epifaunal soft-substrate brachiopods than the bioturbated clayey sandstones facies (SF1). The latter facies is probably more closely comparable to soft ground in the terminology proposed by Goldring (1995).

7. Discussion and conclusion

This study reveals a higher benthic diversity than that described by previous authors in the lower part of the Kermeur Formation, especially for trilobites, which have not been reported before. According to the benthic association models proposed for the Ordovician (Fortey and Owens, 1978, 1987; Henry, 1989; Vidal, 1998), the taxonomic composition and diversity of the complete assemblage (TF1) implies open shelf settings. Assuming that this is a composite assemblage, the very low diversity of the autochthonous fraction (i.e., *Colpocoryphe* and *Aristocystites*) could be consistent with a nearshore assemblage (Henry, 1989; Westrop and Adrain, 1998; Turvey, 2005; Botting and Muir, 2008) but not with this taxonomic composition. In fact, the genus *Colpocoryphe*, which is numerically dominant in grade TF1a, usually occurs in relatively deep open shelf environments characterized by fine-grained sediments (Hammann, 1983; Vidal, 1998). Certain species with reduced eyes, such as *Colpocoryphe taylorum* or *C. inopinata*, were even adapted to the more distal environments of the outer shelf (Fortey and Owens, 1987; Henry, 1989). On the Crozon Peninsula, the species *C. grandis* is present in the upper part of the Postolonnec Formation (Henry, 1980) in silty clayey facies that are related to a distal shelf environment (i.e., the median part of the inner shelf and the outer shelf; Dabard et al., 2007). Moreover, these trilobites co-occur with *Aristocystites*, a diploporid echinoderm related to low-energy environments in some areas (Parsley, 1990). The other part of the assemblage (grade TF1b), which is either allochthonous

or not according to the interpretation, is an epifaunal assemblage dominated by trinucleids (*Onnia*). This association with numerous trinucleids and dalmanitids is reminiscent of the assemblages described from either the upper part of the Postolonnec Formation (*Crozonaspis chauveli* faunizone, Veryac'h section *in* Henry, 1980, p. 232) or the upper part of the Kermeur Formation (*Crozonaspis dujardini* faunizone, Aber section, *in* Henry, 1980, p. 234). In both cases, the sedimentary facies yielding these assemblages are consistent with distal open shelf environments (Loi and Dabard, 2002; Gorini et al., 2008). The present study shows that, in the Kermeur Formation, these species are present in a bay/lagoon context.

This paradox can be explained by a wider range of environmental tolerance (i.e., depth and granulometry) for these taxa, especially for *Colpocoryphe* and *Aristocystites*, and by environmental conditions that were probably similar to those of deeper open environments. In fact, during the early Katian transgression, the construction of a coastal barrier in neashore settings allowed the establishment of turbidity and hydrodynamic conditions that were close to those of deeper open-shelf environments. Moreover, if the barrier was discontinuous or partially submerged, the chemical conditions (i.e., salinity and oxygenation) in the protected area could be similar too. Thus, the formation of lagoon-barrier systems produced new ecological niches available for colonization by organisms accustomed to deeper shelf environments. This colonization may represent an example of offshore–onshore expansion, which is the inverse of the migration described in the onshore–offshore diversification model of Phanerozoic shelf communities (Jablonski et al., 1983; Sepkovski and Sheehan, 1983; Sepkovski and Miller, 1985; Sepkovski, 1991). In this model, new species originate in shallow settings before spreading into deeper environments.

8. Systematic palaeontology

8.1. Trilobita

Family Calymenidae BURMEISTER, 1843

Subfamily Colpocoryphinae HUPÉ, 1955

Genus ***Colpocoryphe*** NOVÁK *in* PERNER, 1918

Colpocoryphe grandis (ŠNAJDR, 1956)

Figs. 10 A–D Material: numerous specimens preserved as internal and external moulds, complete in most cases; only a few were numbered: LPB 14792 to LPB 14799.

Discussion: the large size of the specimens (8 to 10 cm in length on average, and up to 12 cm), the shape of the terminal axial piece of pygidium with lateral expansions, and the large but shallow vincular furrows on pygidial pleurae that become larger forwards, allow this material to be assigned to *Colpocoryphe grandis* (see Henry, 1980). *Colpocoryphe grandis* occurs in the upper part of the Postolonnec Formation and in the lower part of the Kermeur Formation on the Crozon Peninsula, without apparent variation in morphology between these two different formations. In the Kermeur Formation, this taxon occurs as complete exoskeletons and exuviae scattered in SF1, and scarce disarticulated sclerites in lenticular shell concentrations of SF2.

Family Trinucleidae HAWLE and CORDA, 1847

Subfamily Marrolithinae HUGHES, 1971

Genus ***Onnia*** BANCROFT, 1933

Onnia seunesi ? (KERFORNE, 1900)

Figs. 10 E, H

Material: six cephala, preserved as incomplete internal and external moulds. LPB 14800 to LPB 14805.

Discussion: in spite of the missing pygidium and thorax, the shape of the fringe and the position of the girder on the lower lamella allow this material to be assigned to the genus *Onnia* (see Ingham, 1974): from the postero-lateral angle, the girder begins between the first and second row of pits, then curves inward and runs between the second and third row of pits. Among the two *Onnia* species described from the Upper Ordovician of the Armorican Massif (see Lebrun, 1994), *O. seunesi* is most closely related to material from the Kermeur Formation, as the latter shows an occipital spine. Nevertheless, the assignment to *Onnia seunesi* remains doubtful as all studied specimens are broken. They occur in sedimentary facies SF1 in the lower part of the Kermeur Formation, Veryac'h section.

Family Dalmanitidae VOGDES, 1890

Subfamily Zeliskellinae DELO, 1935

Genus ***Zeliskella*** DELO, 1935

***Zeliskella* (*Zeliskella*)** DELO, 1935

***Zeliskella* (*Zeliskella*)** sp.

Figs. 10 G–J Material: one cephalon, preserved as incomplete internal and external moulds, LPB 14806 a, b, and one pygidium, internal mould, LPB 14807.

Discussion: the shape of the glabella (Fig. 10 G) and glabellar furrows (S2, S3), as well as the size and position of eyes, the pit on the frontal lobe of the glabella, the apparent lack of genal spines and tubercle on the occipital ring, are all characteristics shared with *Z. (Zeliskella)*, particularly the slightly earlier species *renaudae* HENRY, 1980. Nevertheless, the posterior furrow of the cephalon stops laterally in the case of *Z. renaudae* (see Henry, 1980), whereas it continues on the free cheek of the single cephalon collected from the base of the Kermeur Formation. Considering this difference and the lack of some exoskeleton parts (particularly, the anterior part of the cephalon and the end-part of the pygidium), a specific assignment is

not possible. Although the internal mould of the pygidium (Fig. 10 J) is poorly preserved, its morphology is compatible with the species cited above. *Zeliskella* (*Zeliskella*) sp. occurs as scarce exoskeleton parts that are isolated and scattered in SF1.

Subfamily uncertain

Phacopidina BANCROFT, 1949

Phacopidina sp.

Fig. 10 F

Material: two cephala preserved as internal moulds, LPB 14808 and 14809 (incomplete).

Discussion: the glabellar furrows S2 and S3 are shallow and less marked than the S1 furrows; S2 furrows are concave backward in the shape of an arc; the S3 furrows are sinuous and convergent backward. These features, added to the shape of the glabella, the position and size of the eyes, as well as the course of the preocular suture - slightly in front but closely following the frontal lobe of the glabella - are consistent with the genus *Phacopidina*. This material is consistent with *Phacopidina micheli* (TROMELIN, 1877), Llanvirn–Lower Caradoc from the Armorican Massif (Henry, 1980), but more material (especially pygidia) is needed to propose a reliable specific assignment. In the Kermeur Formation, *Phacopidina* sp. occurs as scarce exoskeleton parts that are isolated and scattered in SF1.

Family Cheiruridae SALTER, 1864

Subfamily Eccoptochilinae LANE, 1971

Genus ***Eccoptochile*** HAWLE and CORDA, 1847

Eccoptochile sp.

Fig. 10 I

Material: one incomplete pygidium, internal mould, LPB 14810.

Discussion: this pygidium, collected from the base of the Kermeur Formation, in SF1, is referred to *Eccoptochile*. The species of this genus described either in the Armorican Massif (Henry, 1980) or Spain (Hammann, 1974, 1976) are chiefly distinguished by their cephalic morphology, therefore a specific assignment is not possible from this single specimen.

8.2. Echinodermata

Class Diploporita MÜLLER, 1854

Superfamily Aristocystitida NEUMAYR, 1889

Family Aristocystitidae NEUMAYR, 1889

Genus ***Aristocystites*** BARRANDE, 1887

Aristocystites sp.

Fig. 11 A–C

Material: four thecae preserved, one as an internal mould LPB 14811, and three as incomplete external moulds LPB 14812 to 14814.

Discussion: on the external moulds, the thecae are ovoid in shape and more than 10 cm long. The thecal plates are well sized (≥ 5 mm), relatively hexagonal in shape and more or less regularly arranged. They show dense vermicular openings but no tubercle is observed. These features indicate that the specimens from the base of the Kermeur Formation should be assigned to the genus *Aristocystites*, and are particularly reminiscent of *A. bohemicus* BARRANDE, 1887 (see Parsley, 1990). Since neither holdfasts nor oral faces are observed on the collected specimens, the specific assignment remains uncertain. In the Kermeur Formation, *Aristocystites* sp. is preserved as complete thecae and isolated thecal plates scattered in the highly bioturbated SF1, and then only as thecal plates in lenticular shell concentrations of SF2 together with brachiopod valves.

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844
845 **Figures captions**

Fig. 1. Location of the Kermeur Formation outcrops in the Armorican Massif (Crozon Peninsula).

Fig. 2. Ordovician deposits in the Veryac'h section (Crozon Peninsula), with global and British stratigraphic stages (assigned from Paris, 1990; Bourahrouh, 2002; Webby et al., 2004).

Fig. 3. Lithostratigraphic column of the Veryac'h section, from the upper part of the Postolonnec Formation to the lower part of the Kermeur Formation. Vertical evolution of sedimentary environments from SF0 to SF4. Location of the fossiliferous levels (shown by a grey line) and related taphofacies.

Fig. 4. Bioturbated clayey sandstone SF1 with some preserved sandy layers (arrows in A) and bioturbation (B). Bioturbated sandy mudstone SF2 with equilibrichnia structures (C) and preserved black clayey mudstone (arrow in D).

Fig. 5. Bioturbated heterolithic SF3. General views (A and C) and details showing lenticular to flaser beddings (D, F, G), current ripples with clay drapes on the top surface of a sandy bed (B), current ripples with opposite directions (E), waves ripples with flattened crests overlain by current ripples at the top of a sandy bed (D). Bioturbated heterolithic (SF3) and quartz-arenite (SF4) facies (F, G). Skolithos burrows filled with clayey material (arrow in F). Puddle with wave ripples (arrow) in the quartz-arenite SF4 (H).

Fig. 6. General view of the quartz-arenite SF4 (A) and details showing the concave scours in

the sandy beds (arrows in B) and swaley cross-stratification (D). Lateral transition from SF3 to SF4 (C).

Fig. 7. Depositional model for the lower part of the Kermeur Formation. Distribution of the sedimentary (SF) and taphonomic (TF) facies from continental (X) to open marine (Y) domains.

Fig. 8. Evolution in space (X–Y) and time of the distribution of sedimentary facies in the Veryac'h section during the transgressive phase. P1, P2 and P3 represent the adjustment barrier-lagoon profiles related to the sea-levels (L1, L2, L3) at different times. The SF0 occurs in the transgressive surface.

Fig. 9. Taxonomic and taphonomic composition of fauna from the lower part of the Kermeur Formation. (A) Taphofacies 1, strictly associated with SF1, is characterized by a random dispersion of specimens. Depending on the taxa, skeletons are either preserved whole and articulated (grade TF1a) or, on the contrary, systematically disarticulated and often fragmented (grade TF1b). (B) In taphofacies 2, strictly associated with SF2, fossil remains are disarticulated and preserved in lenticular shell concentrations.

Fig. 10. Selected specimens from the lower part of the Kermeur Formation (SF1 and SF2), Veryac'h section, Crozon Peninsula, France. Scale bar: 0.5 cm.
(A–D) *Colpocoryphe grandis* (ŠNAJDR, 1956);
(A) internal mould of a complete exoskeleton, LPB 14792; (B) internal mould of a moult, with dorsal view of the connected thorax and pygidium and ventral view of the librigenae,

(the cranidium is under librigenae), LPB 14795; (C) internal mould of a pygidium, LPB 14793; (D) rubber cast of an external mould of a pygidium, LPB 14794.

(E, H) *Onnia seunesi* ?;

(E) internal mould of cephalon, LPB 14804; (H) internal mould of cephalon, LPB 14800.

(F) *Phacopidina* sp., internal mould of cephalon, LPB 14808.

(G, J) *Zeliskella* (*Zeliskella*) sp.; (G) internal mould of incomplete cranidium, LPB 14806a; (J) internal mould of incomplete pygidium, LPB 14807.

(I) *Eccoptochile* sp., internal mould of pygidium, LPB 14810.

(K) *Triplesia* cf. *T. simplex* HAVLÍČEK, 1971, internal mould of ventral valve, LPB 14126.

(L, M) *Drabovia pentagonomya* HAVLÍČEK, 1971; (L) internal mould of dorsal valve, LPB 14110; (M) internal mould of ventral valve, LPB 14108.

(N, O) *Tafilaltia destombesi* HAVLÍČEK, 1970; (N) internal mould of dorsal valve, LPB 14092; (O) internal mould of ventral valve, LPB 14091.

Fig. 11. *Aristocystites* sp., diploporid from the lower part of the Kermeur Formation, Veryac'h section, Crozon Peninsula, France. Scale bar: 0.5 cm.

(A) internal mould of theca, LPB 14811;

(B) one isolated thecal plate with filling of diplopores, dichotomous at each end, LPB 14812;

(C) external mould of theca, LPB 14813.

Fig. 1

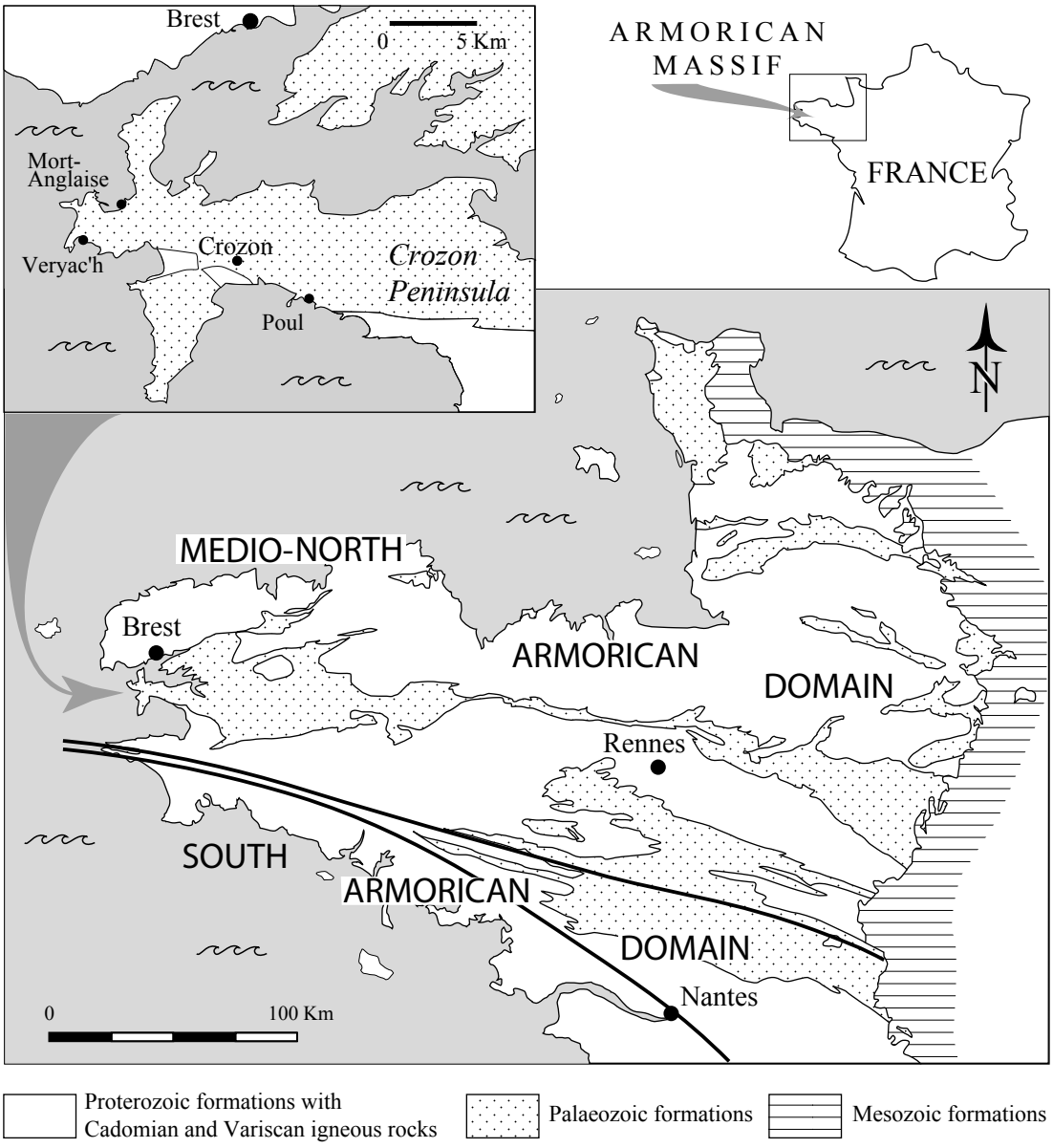

Brest
0
5 Km
Mort-
Anglaise
Veryac'h
Crozon
Crozon
Peninsula
Poul
ARMORICAN
MASSIF
FRANCE
N
MEDIO-NORTH
Brest
ARMORICAN
DOMAIN
Rennes
SOUTH
ARMORICAN
DOMAIN
Nantes
0
100 Km
Proterozoic formations with
Cadomian and Variscan igneous rocks
Palaeozoic formations
Mesozoic formations

Fig. 2

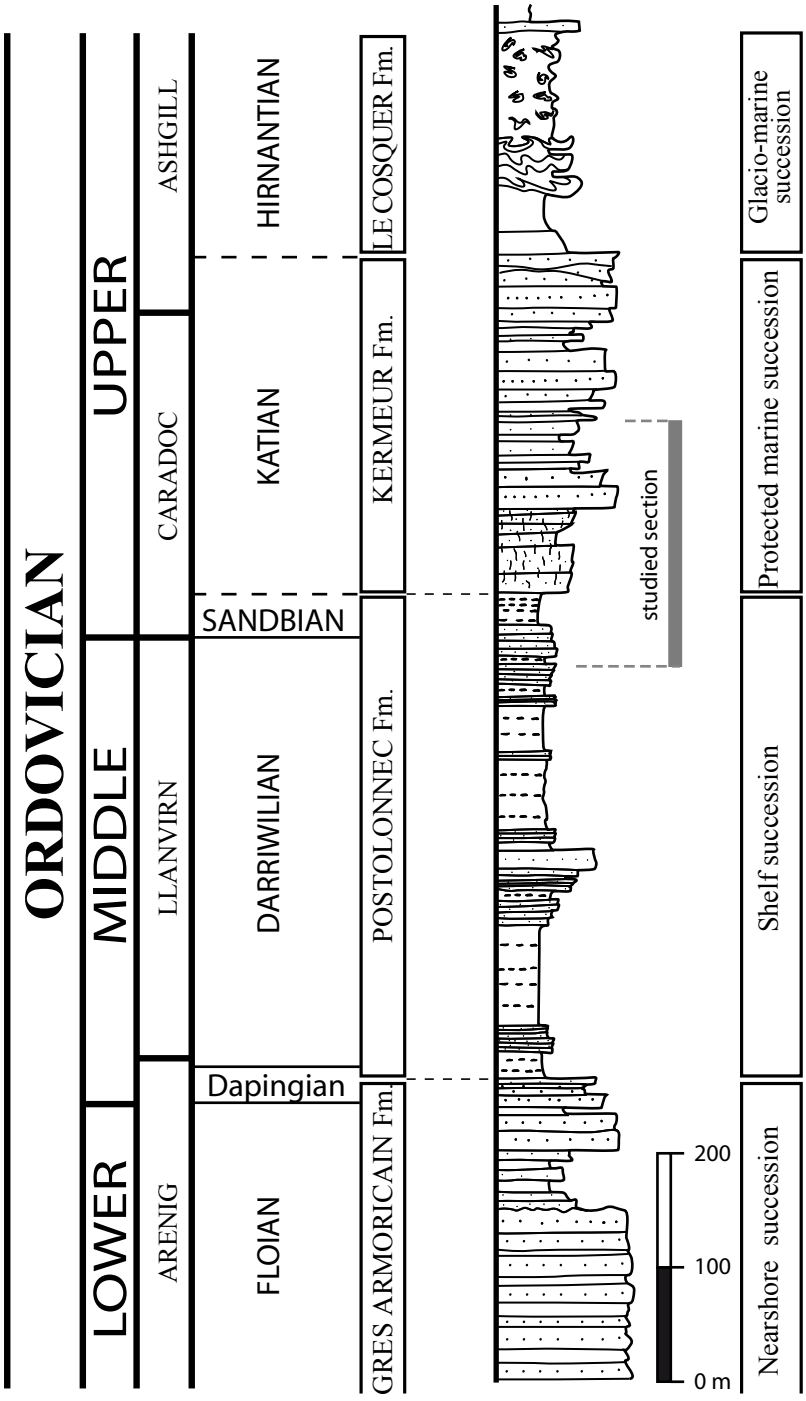

ORDOVICIAN
LOWER
MIDDLE
UPPER
ARENIG
LLANVIRN
CARADOC
ASHGILL
FLOIAN
DARRIWILIAN
KATIAN
HIRNANTIAN
Dapingian
SANDBIAN
GRES ARMORICAIN Fm.
POSTOLONNEC Fm.
KERMEUR Fm.
LE COSQUER Fm.
studied section
200
100
0 m
Nearshore succession
Shelf succession
Protected marine succession
Glacio-marine succession

Fig. 3

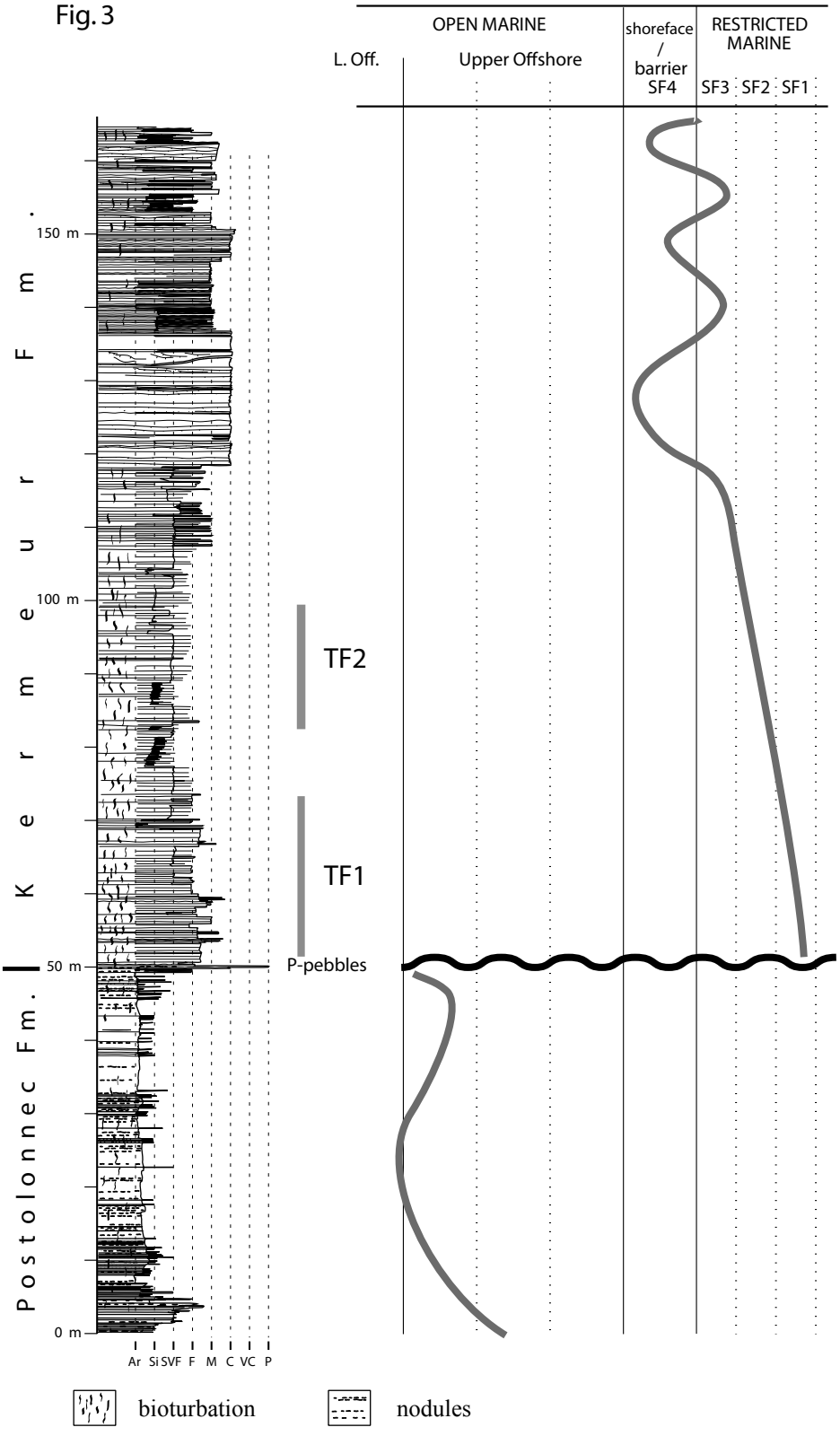
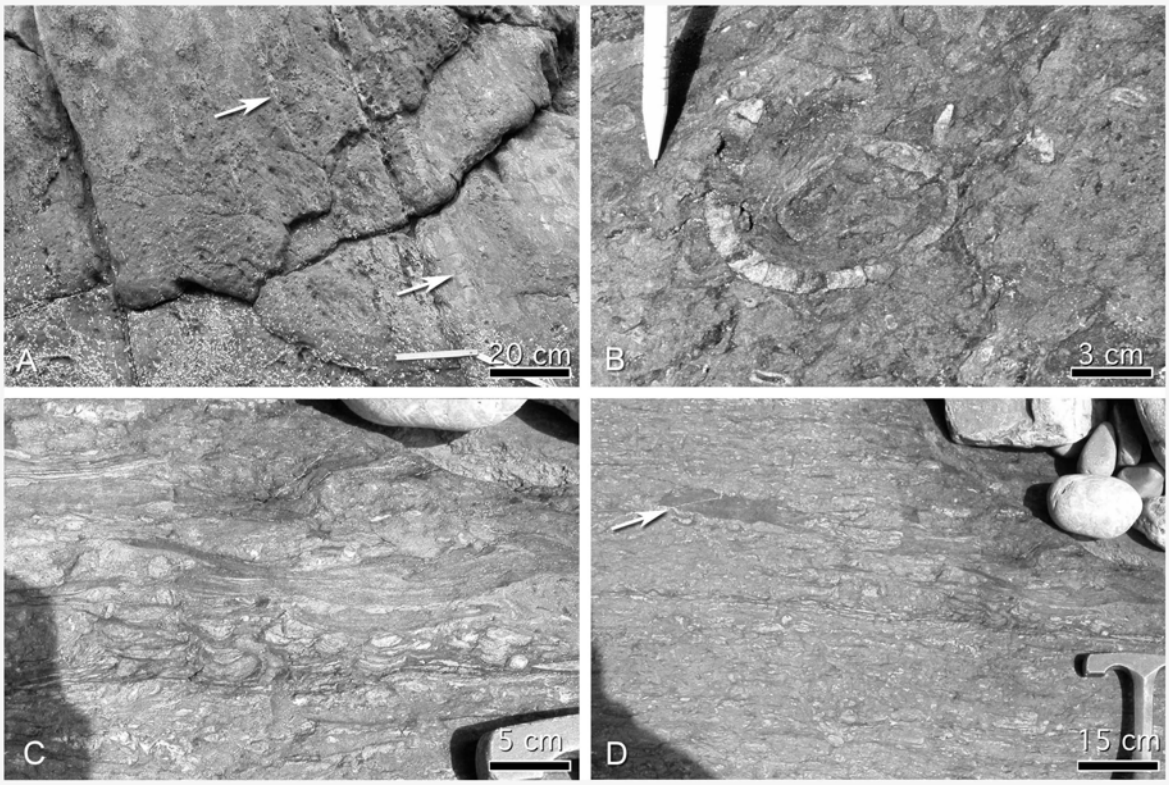
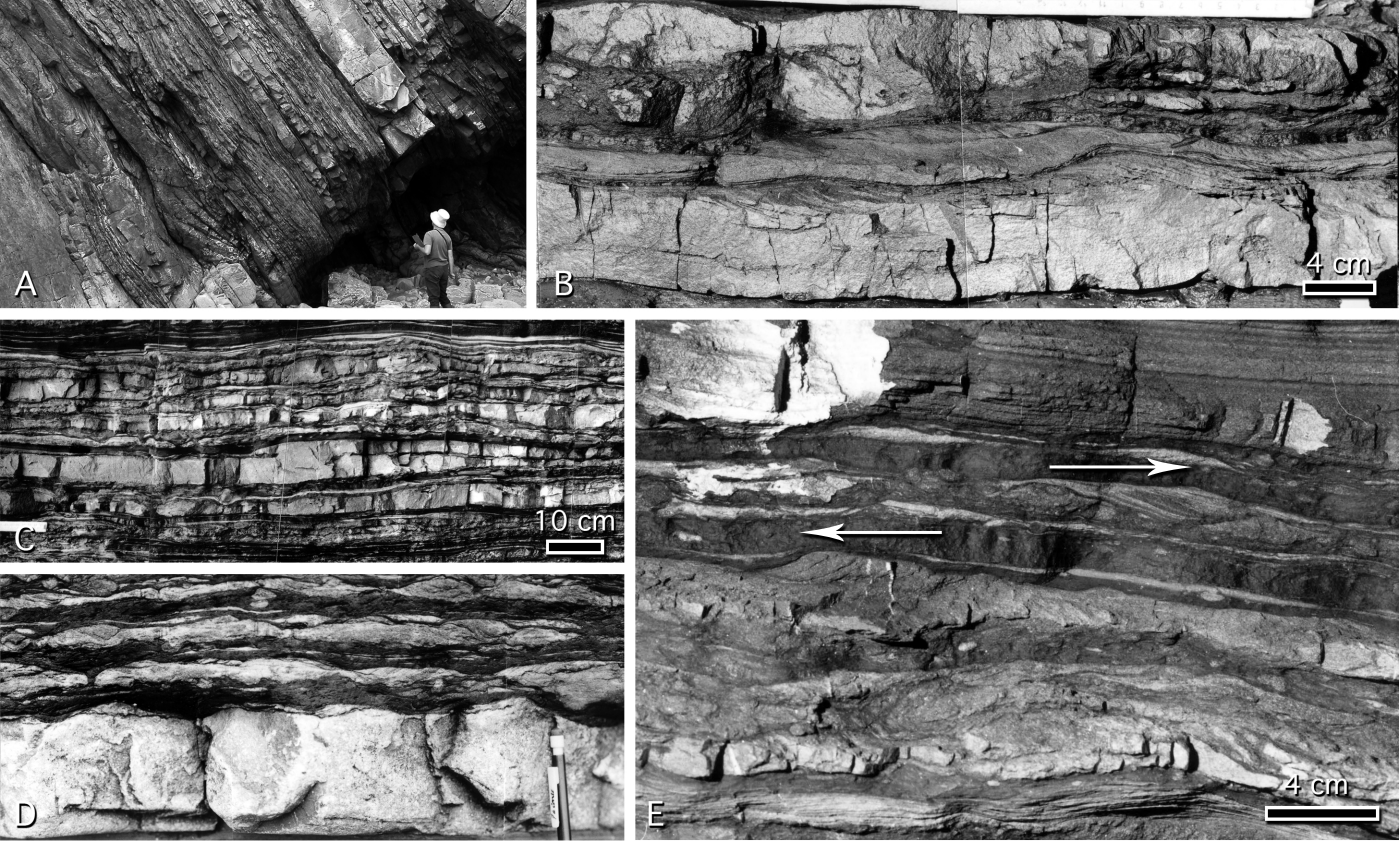
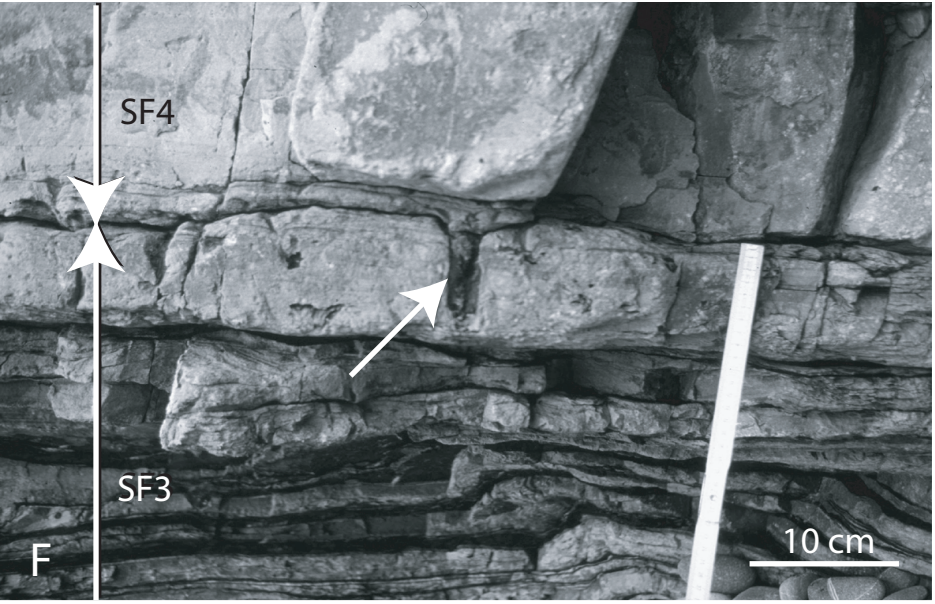
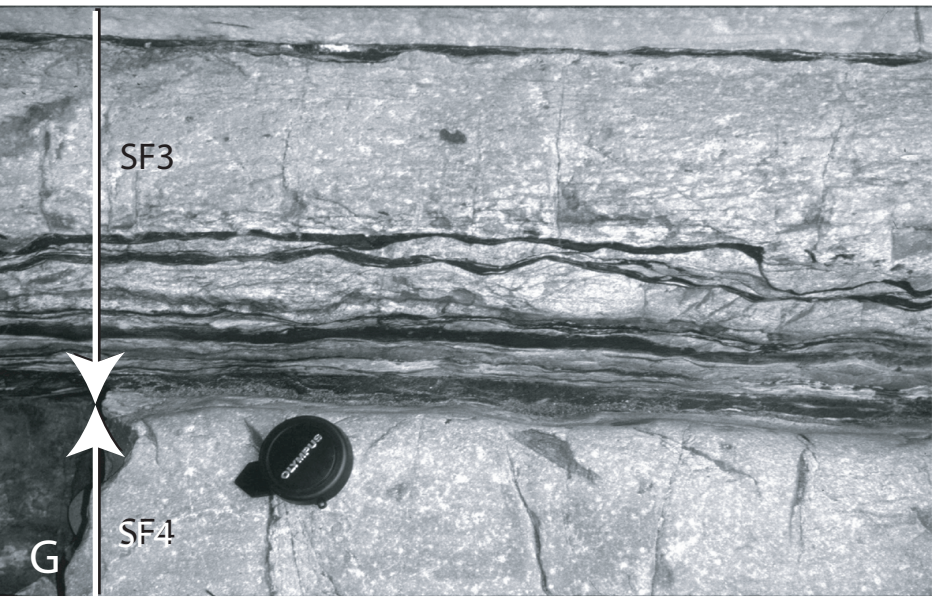

OPEN MARINE
L. Off.
Upper Offshore
shoreface / barrier SF4
RESTRICTED MARINE
SF3
SF2
SF1
Kermeur Fm.
Postolonnec Fm.
150 m
100 m
50 m
0 m
TF2
TF1
P-pebbles
Ar Si SVF F M C VC P
bioturbation
nodules

Fig. 4




A
B
4 cm
C
10 cm
D
E
4 cm


SF4
SF3
10 cm
F


SF3
SF4
G

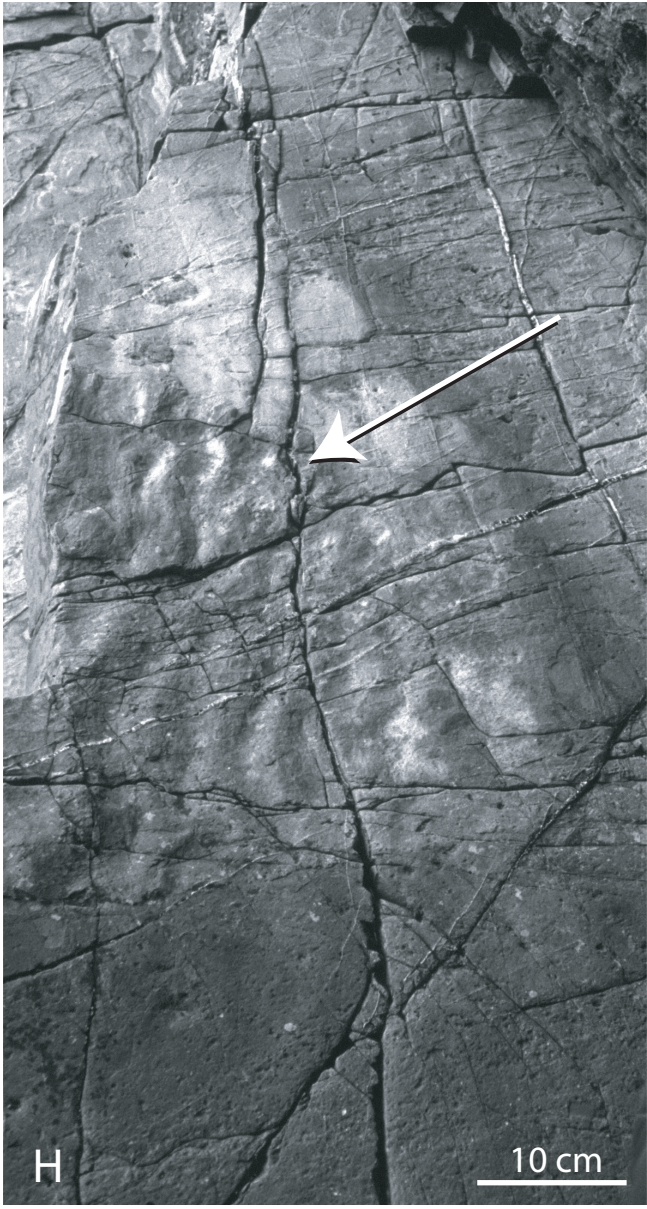

H
10 cm

Fig. 6

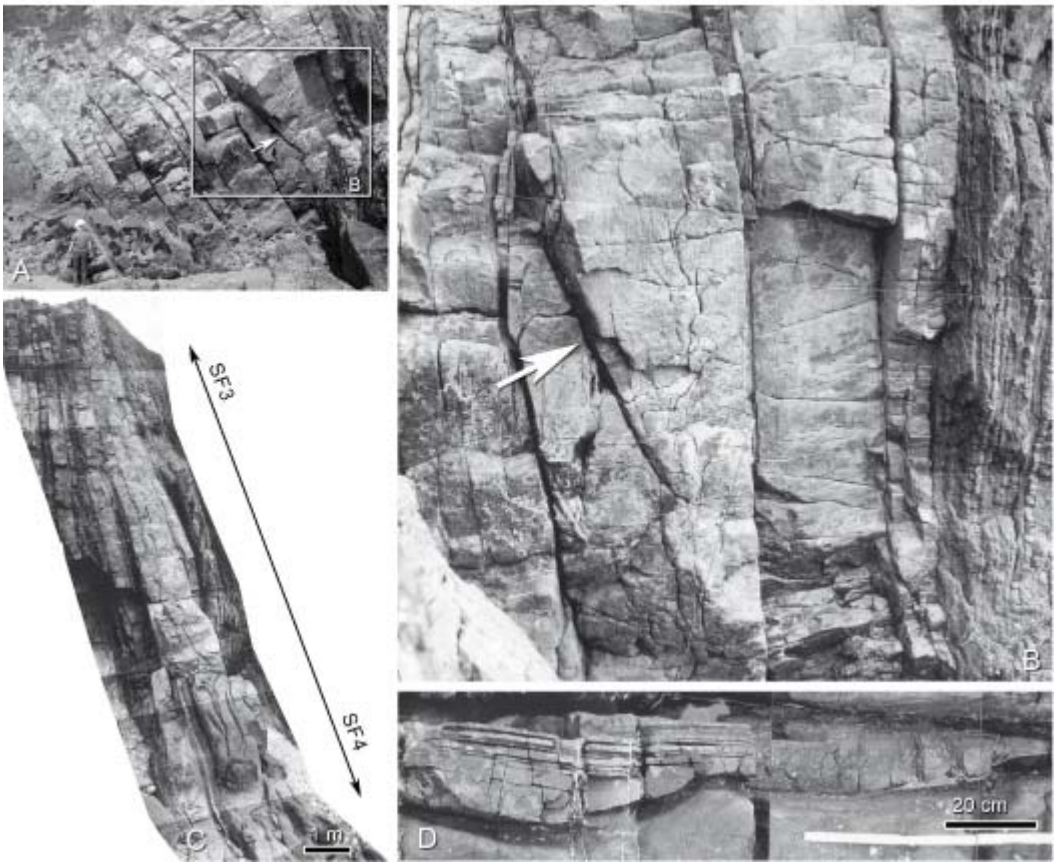


Fig. 7

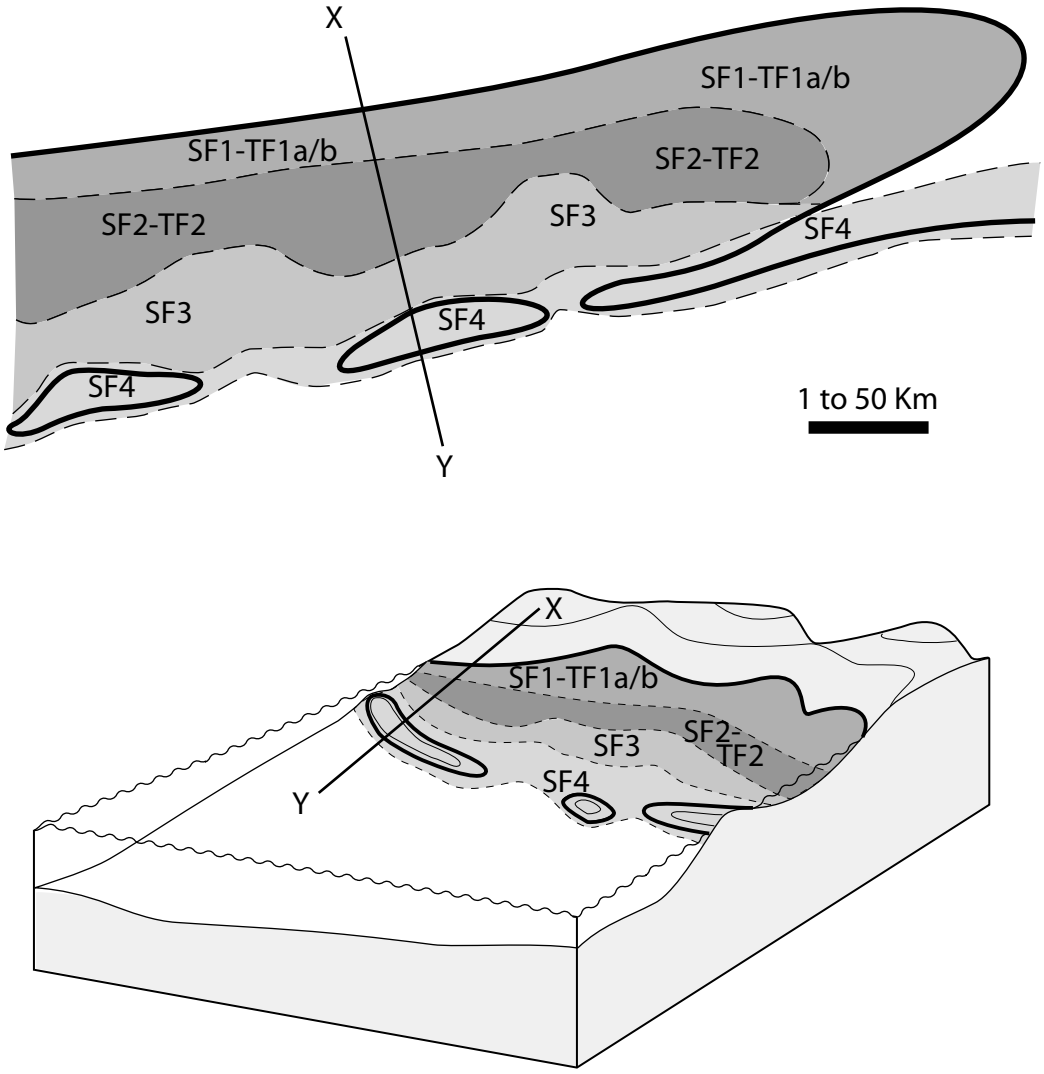

X
Y
SF1-TF1a/b
SF1-TF1a/b
SF2-TF2
SF2-TF2
SF3
SF4
SF3
SF4
SF4
1 to 50 Km
X
Y
SF1-TF1a/b
SF3
SF2-TF2
SF4

Fig. 8

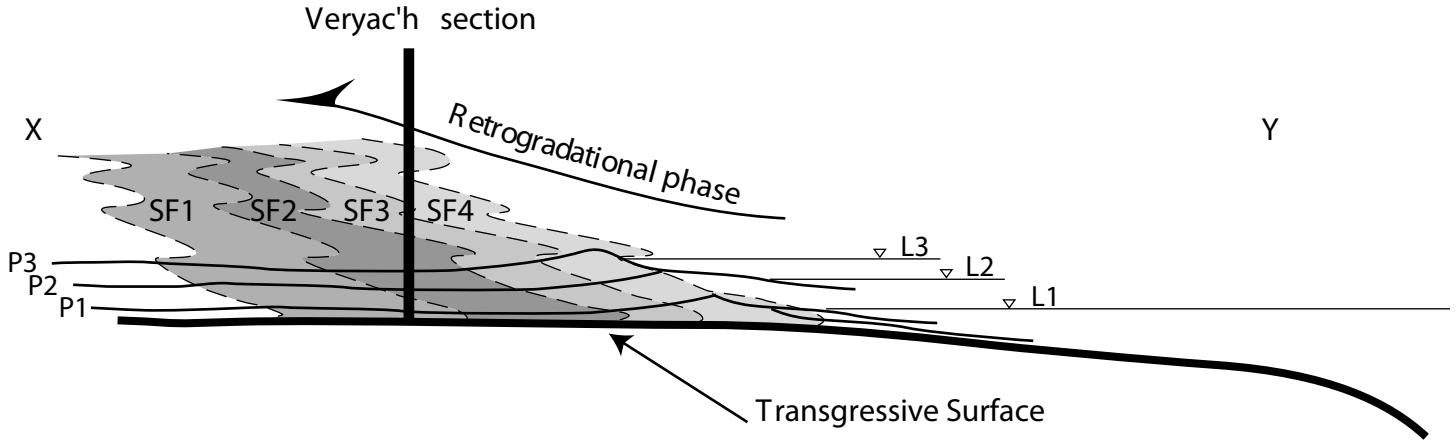

Veryac'h section
X
Y
Retrogradational phase
SF1
SF2
SF3
SF4
P3
P2
P1
L3
L2
L1
Transgressive Surface

Fig. 9

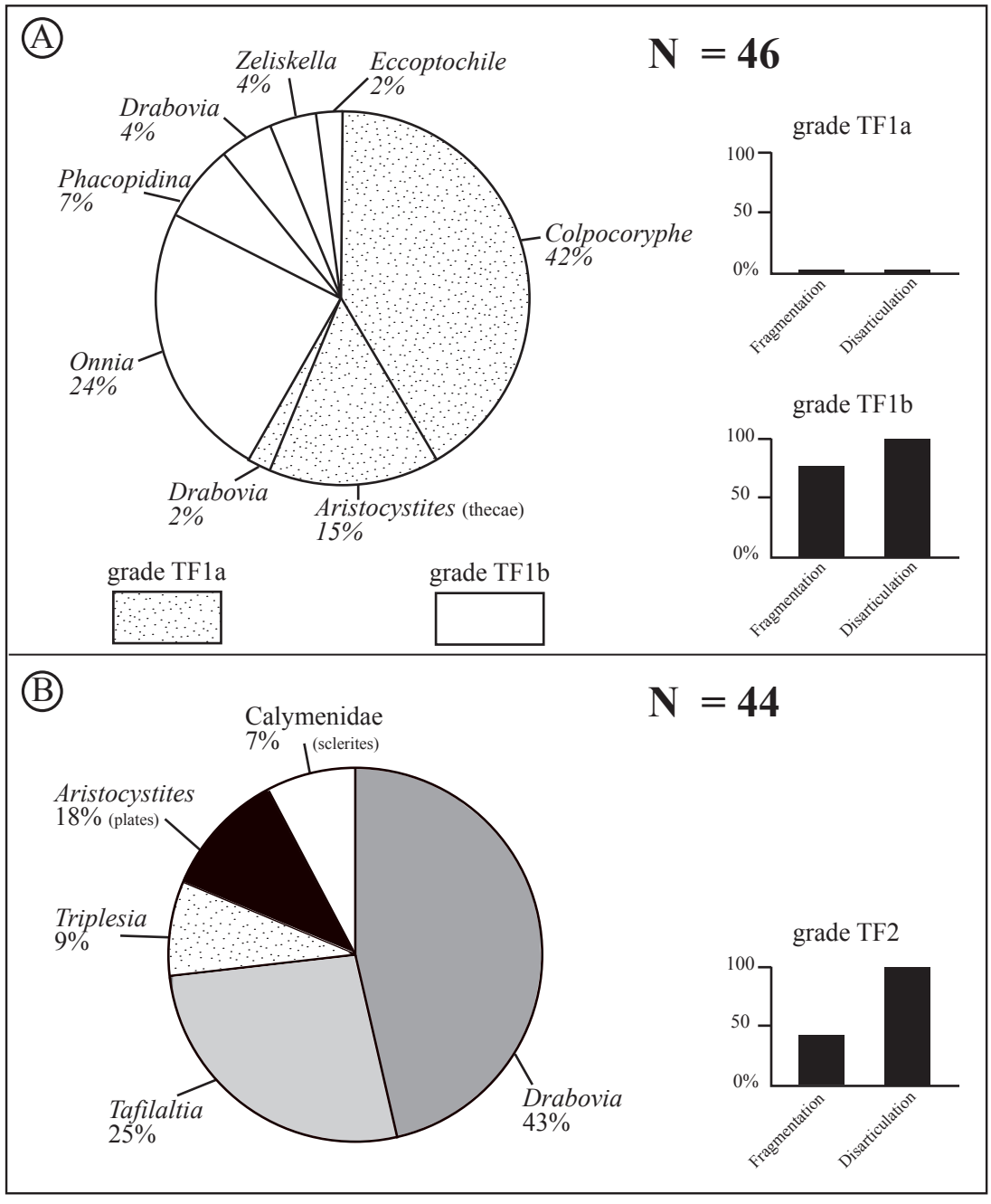

A
N = 46
Zeliskella 4%
Eccoptochile 2%
Drabovia 4%
Phacopidina 7%
Colpocoryphe 42%
Onnia 24%
Drabovia 2%
Aristocystites (thecae) 15%
grade TF1a
grade TF1b
grade TF1a
100
50
0%
Fragmentation
Disarticulation
grade TF1b
100
50
0%
Fragmentation
Disarticulation
B
N = 44
Calymenidae 7% (sclerites)
Aristocystites 18% (plates)
Triplesia 9%
Tafilaltia 25%
Drabovia 43%
grade TF2
100
50
0%
Fragmentation
Disarticulation

Fig. 10

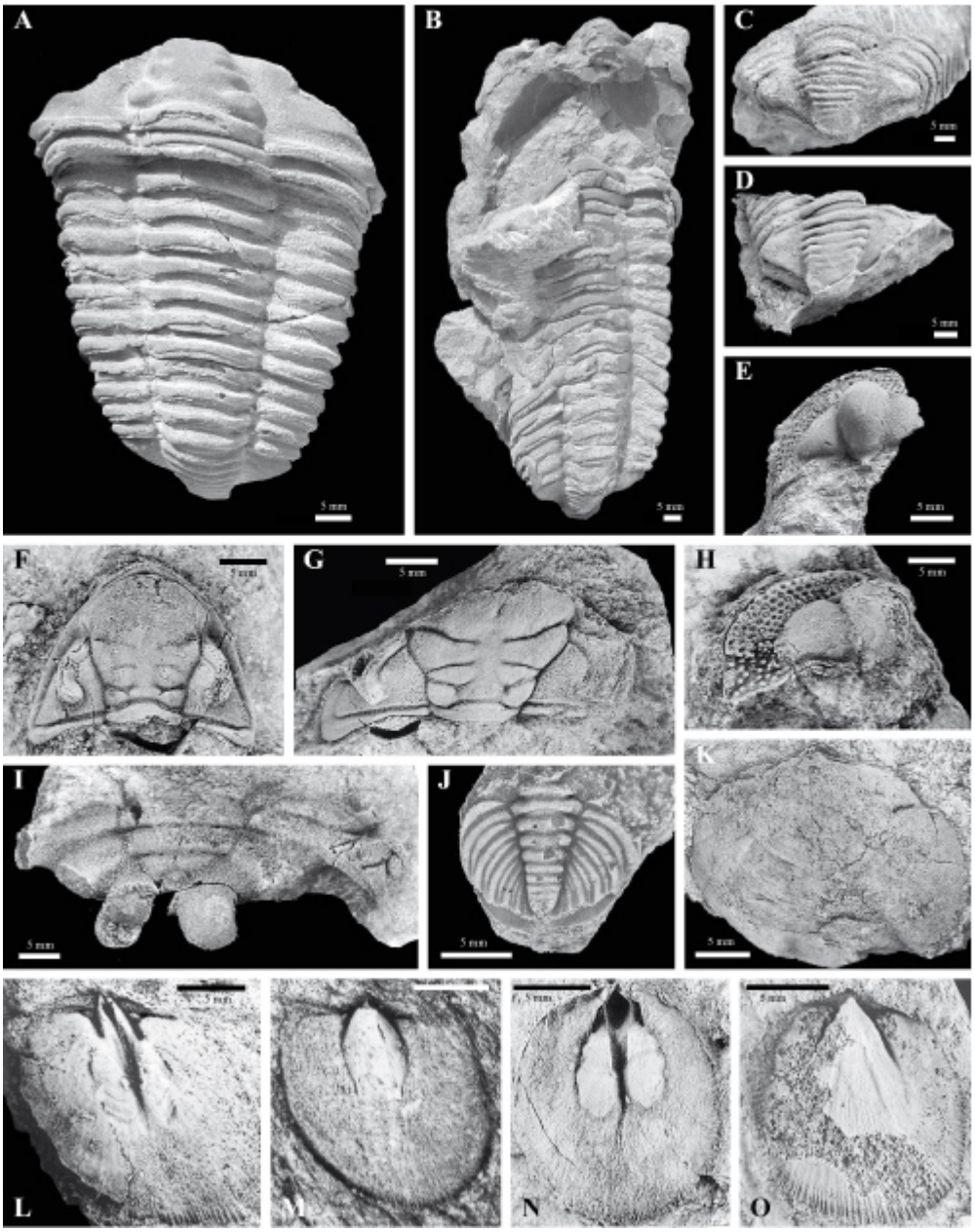


Fig. 11